Comments

COMPARATIVE DEMOGRAPHY OF NEW WORLD POPULATIONS OF THRUSHES (TURDUS SPP.): COMMENT

Paul B. Conn,[1,3] Paul F. Doherty, Jr.,[1] and James D. Nichols[2]

Survival and fecundity are fundamental to the study of evolutionary ecology, as they are two of the key variables influencing the constrained optimization process we call natural selection. Likewise, population managers require accurate estimates of these parameters; along with dispersal, they govern population dynamics (Lack 1954) and thus are essential for predicting population change and the effects of management actions. It can be frustrating, then, when survival is difficult to estimate for certain populations, as in some avian species that exhibit a substantial degree of dispersal.

Accurate estimation of survival has proven to be one of the more difficult problems in avian ecology because of difficult sampling logistics and the potential for emigration from study areas. For instance, survival is confounded with permanent emigration probability in traditional mark–recapture such as Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) models. Thus, failing to account for emigration leads to a negative bias in this type of survival estimator, as Cilimburg et al. (2002) demonstrated nicely in a study of Yellow Warblers.

In an effort to find a suitably robust survival estimator that could be parameterized from commonly available data, Ricklefs (1997) investigated the use of age ratios from the counts of adult (A; ≥ 1 years old) and immature (I; <1 years old) museum collection specimens. Under this approach, survival is estimated by the proportion $\hat{v} = A/(A + I)$ (Ricklefs 1997). Rick-

lefs then used age ratios from museum collections for a number of *Turdus* species to quantify differences in survival across a latitudinal gradient. More recently, Rohwer (2004) used this approach for comparing the demography of several Neotropical migrant warbler species.

Ricklefs' (1997) method is a special case of a time-specific (vertical) life table approach (Seber 1982). Age-specific or dynamic life table approaches used historically to estimate survival rates of migratory birds were typically based on samples of birds marked and released as young in consecutive years and, hence, of known age when recovered as dead in subsequent years (e.g., Hickey 1952, Seber 1971, 1972). Because they are based on marked samples of birds, these life tables did not require all of the assumptions needed for vertical life tables. Nevertheless, numerous authors have cautioned against the use of both types of life tables for survival estimation because of the specific, yet critical, assumptions underlying these approaches (cf. Anderson et al. 1981, Seber 1982, Messier 1990, Clobert and Lebreton 1991, Menkens and Boyce 1993). Some of these assumptions are difficult to test, and those that can be tested have been found to be false for most data sets (e.g., Burnham and Anderson 1979, Anderson et al. 1981, Menkens and Boyce 1993, Bonenfant et al. 2005). For example, natural populations often fluctuate with environmental conditions, so the assumption that $\lambda = 1$ required by vertical life tables is questionable (Seber 1982, Messier 1990, Menkens and Boyce 1993).

The recent resurrection of ad hoc life table estimators by influential avian ecologists (e.g., Ricklefs 1997, Green 2004, Rohwer 2004) suggests that it is appropriate to remind the scientific community of the possible problems associated with these methods. We start by briefly reviewing the estimator proposed by Ricklefs (1997). We then address a number of assumptions required by the age ratio estimator, several of which were not discussed by Ricklefs (1997). In addition, we examine the efficacy of Ricklefs' (1997) variance estimator by formally acknowledging uncertainty about model assumptions. Next, we consider the issue of comparing age ratios across time or space. Finally, we discuss several recently available mark–recapture and mark–recovery estimators, and compare the assumptions underlying these methods to the assumptions underlying age ratios. Although these designs are certainly not a panacea, we argue that these techniques provide the most reliable means currently available to answer questions regarding avian survival and dispersal.

Age Ratio Estimator

Model description

According to Ricklefs (1997), avian survival may be robustly estimated by the age proportion $\hat{v} = A/(A + I)$ when adult and immature age class counts (A and I, respectively) are obtained for a representative sample after the immature age class has attained adult survival probability. As Green (2004) shows, this estimator may be easily derived by noting that

$$N_i = N_{i-1} \times \varphi_{i-1} + (1 - v_i) \times N_i$$

where N_i is the population size of adults (≥ 1 year old) and immatures (<1 year old) at time i, φ_i is survival for adults and immatures from time i to $i + 1$, and v_i is the true proportion of adults in the population. Rearranging this equation results in

$$v_i = \varphi_{i-1} \times N_{i-1}/N_i$$

and thus the proportion of adults in the population equates with survival when $\lambda = 1$. Because the true proportion of adults in the population is rarely known, Ricklefs (1997) considered the problem of sampling adults and immatures. Assuming that adult and immature collection probabilities are the same, Ricklefs (1997) demonstrated that the proportion of adults in a sample of collected individuals was an unbiased estimator of adult survival probability, with a standard error given by $[AI/(A + I)^3]^{0.5}$.

Model assumptions

Ricklefs (1997) identified a number of assumptions that must hold if the age ratio survival estimator is to be unbiased. In general, λ, the finite rate of population change, must be 1 and cannot fluctuate; immatures need to have attained adult survival probabilities by the time of sampling; immature collection probability (p_I) must equal adult collection probability (p_A); senescent decline in survival probability cannot occur; breeding must be seasonal; and plumage maturation must be time invariant and occur between the first and second time that an individual is exposed to sampling effort. Ricklefs (1997) found that violations of each of these assumptions alone did not substantially bias his age ratio survival estimator, but he did not attempt to employ several of them at once, nor did he include uncertainty about the validity of these assumptions in his accompanying variance estimation formula.

Rohwer (2004) acknowledged possible problems with the equivalence of adult and immature detection probabilities, noting that adult male migratory warblers are more likely to have mates than immatures and thus are less likely to sing than immatures. In this case, collectors are more likely to detect, and therefore collect, immatures. In other passerine species, adults sing more often than immatures, leading to an opposite sort of collection bias. Also, when adults arrive on breeding grounds before immatures, they may have access to higher quality habitat. If collectors target high-density areas, museum collections may be adult-biased (Rohwer 2004).

Bias from aging error

While not explicitly considered by Ricklefs (1997), aging error can bias survival estimators obtained from age ratios. For instance, Green et al. (2001) developed an aging index for Corncrakes (*Crex crex*) based on the sum of angles of secondary remiges from known-age individuals. Green et al. (2001) showed that the distribution of the index for immatures and adults could be represented by overlapping normal distributions. If aging uncertainty is not incorporated into the age ratio estimator (cf. Green 2004), one must assume a threshold index value in order to assign age. The magnitude of bias then depends on φ, the adult survival probability, θ^A, the proportion of adults incorrectly aged as immatures, and θ^I, the proportion of immatures incorrectly aged as adults. If all other assumptions of age ratio estimators are met (see Appendix A), bias can be shown to be

$$B(\hat{\varphi}) = \theta^I - \varphi \, (\theta^I + \theta^A).$$

Bias in the survival estimator can be substantial for even relatively small values of θ^A and θ^I (Table 1).

Bias from immigration and emigration

Rohwer (2004) argued that conventional mark–recapture estimators are inappropriate for estimating survival in populations exhibiting a large degree of breeding dispersal, because survival is confounded with permanent emigration. We anticipate that ecologists may use this reasoning to justify the use of age ratios for survival estimation. However, as Rohwer (2004) admits, immigration and emigration also may bias age ratio survival estimators if sampling is not conducted across the entire range of the population.

Ricklefs (1997) maintained that a portion of the avian population balance equations could often be written as

$$N_{i+1}^A = (N_i^A + N_i^I)\varphi_i$$

where N_i^A is the number of adults in the population at time i, N_i^I is the number of immatures in the population at time i, and φ_i is adult survival rate. This expression implicitly assumes that population sizes are tabulated after immatures have attained adult survival. If $\lambda = 1$, then the age ratio estimator is unbiased for φ_i.

Now consider the situation in which a proportion of the population leaves the study area each year. One method for dealing with this situation is to incorporate

TABLE 1. Bias in the age ratio survival estimator, $B(\hat{\varphi})$, under different scenarios.

A) Errors in aging				B) Imbalance in emigration and immigration			
θ^A	θ^I	φ	$B(\hat{\varphi})$	π_i	φ_i	F_i	$B(\hat{\varphi})$
0.1	0.1	0.8	−0.06	1.5	0.8	0.8	0.08
0.1	0.1	0.6	−0.02	1.5	0.6	0.8	0.06
0.1	0.1	0.4	0.02	1.5	0.4	0.8	0.04
0.1	0.0	0.8	−0.08	1.5	0.8	0.5	0.20
0.1	0.0	0.6	−0.06	1.5	0.6	0.5	0.15
0.1	0.0	0.4	−0.04	1.5	0.4	0.5	0.10
0.0	0.1	0.8	0.02	0.5	0.8	0.8	−0.08
0.0	0.1	0.6	0.04	0.5	0.6	0.8	−0.06
0.0	0.1	0.4	0.06	0.5	0.4	0.8	−0.04
0.2	0.2	0.8	−0.12	0.5	0.8	0.5	−0.20
0.2	0.2	0.6	−0.04	0.5	0.6	0.5	−0.15
0.2	0.2	0.4	0.04	0.5	0.4	0.5	−0.10
0.0	0.2	0.8	0.04				
0.0	0.2	0.6	0.08				
0.0	0.2	0.4	0.12				
0.2	0.0	0.8	−0.16				
0.2	0.0	0.6	−0.12				
0.2	0.0	0.4	−0.08				

Notes: In Part A (left), adults are mistakenly aged as immatures with probability θ^A, immatures are mistakenly aged as adults with probability θ^I, and true adult survival is equal to φ. In part B (right), adult emigration $(1 - F_i)$ does not balance adult immigration. A value for π_i of 0.5 indicates that there are half as many immigrants as emigrants, whereas a value of 1.5 indicates that there are two-thirds as many emigrants as immigrants.

a fidelity parameter, F_i, into the population balance equation, such that

$$N^A_{i+1} = (N^A_i + N^I_i)\varphi_i F_i.$$

If immigration also takes place, and is expressed relative to the number of individuals that emigrate from the study area, we may write

$$N^A_{t+1} = (N^A_i + N^I_i)\varphi_i F_i + \pi_i(N^A_i + N^I_i)\varphi_i(1 - F_i) \quad (1)$$

where π_i represents the relative intensity of immigration for year i subject to the constraint

$$0 \le \pi_i \le \frac{1 - \varphi_i F_i}{\varphi_i(1 - F_i)}.$$

For instance, if $\pi_i = 1$, then the gain to the adult population from immigration completely offsets losses from emigration. Alternatively, if $\pi_i < 1$, then the number of emigrants exceeds immigrants; if $\pi_i > 1$, the number of immigrants exceeds emigrants.

Under the assumption of a stable population, the proportion of individuals with adult plumage in the population at time $i + 1$ is

$$v_{i+1} = \varphi_i F_i + \pi_i\varphi_i (1 - F_i).$$

Thus the expected bias of the age ratio survival estimator is as follows:

$$B(\hat{\varphi}_i) = \varphi_i(F_i + \pi_i - \pi_i F_i - 1).$$

Although bias is zero when immigration exactly offsets emigration, the bias can be substantial when emigration and immigration are unbalanced (Table 1). This could occur, for example, when collectors target habitats that may attract a substantial number of adult immigrants (in some cases, high-quality habitats and in others, dispersal sinks). Perhaps most important, it is seldom possible to draw inferences about immigration and emigration processes occurring at the time of collection of most age ratio data. Thus, the very factor that was claimed to motivate the use of age ratios to estimate survival rate (Rohwer 2004) can produce substantial bias in these estimates.

Uncertainty analysis

An additional feature of the age ratio survival estimator is that there is no capacity to incorporate uncertainty about model assumptions into the estimation framework. However, the implication of uncertainty can be examined by considering a hypothetical example. For instance, assume that the dynamics of a population can be reasonably summarized with Eq. 1 and the difference equation:

$$N^I_{i+1} = \lambda_i(N^A_i + N^I_i) - N^A_{i+1}.$$

For fixed initial population sizes and survival rates, we can examine the effects of uncertainty in λ_i, F_i, and π_i on the number of adults and immatures in the population at the next time step by formulating prior distributions for these parameters and using parametric bootstrapping to determine a range of possible outcomes. If we additionally impose an observation model on top of simulated population dynamics, we can simultaneously explore the consequences of differing collection probabilities. Binomial models for the counts of adults (A_i) and immatures (I_i) are appropriate in this context, with indexes N^A_i and N^I_i and success (i.e., collection) probabilities p^A_i and p^I_i, respectively.

As a hypothetical example, let the initial population under consideration have 1000 adults and 1000 immatures, and let true survival be 0.5. We can express uncertainty about additional parameters by assuming uniform prior distributions. For instance, allowing λ to take on values in [0.8, 1.2], F_i to be in [0.6, 1.0], π_i to be in [0.6, 1.4], p^A_i to be in [0.15, 0.25], and p^I_i to be in [0.15, 0.25], yields a bootstrap distribution for expected age ratios. Although unbiased, the standard error of this distribution (0.085) far exceeds 0.025, the simple binomial sampling variance given by Ricklefs (1997). Thus, by admitting uncertainty about model assumptions, we also admit confidence intervals on survival more than three times as wide.

Although this example illustrates that an inflated variance accompanies realistic acknowledgement of uncertainty, we purposefully selected the expected values for each distribution so that the age ratio survival estimator is still unbiased. This need not be the case. For instance, Jones et al. (2004) reported an apparent survival probability of 0.49 and $\lambda = 0.73$ for Cerulean Warblers (*Dendroica cerulean*) breeding in Ontario, Canada. Incorporating these point estimates into the uncertainty analysis yields an expected age ratio of 0.67, and thus a bias of 0.18, in addition to a heightened variance (SE = 0.06).

Comparing age ratios across time or space

Rohwer (2004) suggested that differences in age ratios between populations or species could be used as valid comparisons of survival even if individual age ratios were biased estimators. One reviewer of the present manuscript mirrored this view, contending that the patterns of variation in Ricklefs' (1997) comparative survival analysis of *Turdus* were undoubtedly real, even though the absolute estimates could be questioned. Although Ricklefs' results correspond nicely to predictions of time-honored ecological hypotheses, we would argue that it is easy to construct scenarios in which his comparisons could be wrong. For instance, if λ, immigration–emigration patterns, or sampling processes varied systematically across a latitudinal gradient, it would be possible to come up with the same patterns produced from Ricklefs' age ratios, even if adult survival was equal across populations.

MARK–RECAPTURE METHODOLOGY

Rohwer (2004) argued that ''Plot-based recapture studies will never be practical for estimating survival in birds that are difficult to mark and recapture, and will always underestimate survival when long distance breeding dispersal occurs.'' Statements such as these betray a lack of understanding about the substantial progress in mark–recapture methodology that has been made in recent years (Appendix B). For instance, several mark–recapture models allow for separate estimation of survival from permanent or random emigration if auxiliary observations such as band recoveries (Burnham 1993) or resightings (Barker 1997) are available outside the study area where mark–recapture effort is applied. Separation of survival and emigration is also possible if a sample of individuals is tracked by telemetry (Powell et al. 2000), or if sampling is conducted across multiple sites, as with multistate mark–recapture (Arnason 1973, Brownie et al. 1993, Schwarz et al. 1993). All of these approaches have been applied successfully to studies of avian survival (cf. Appendix B). This is not to say that there will always be a practical means for survival estimation, especially in cases of complex emigration dynamics or when sampling resources are limited. Still, we are optimistic that current developments in sampling technology will only help to increase the affordability and scope of possible research avenues. For instance, identification of individuals by genotyping feathers or nest material (e.g., Pierce et al. 1997) may prove to be an important source of data for developing more cost-effective estimators. In addition, as technology progresses, the affordability and size of telemetry devices should both decrease.

AGE RATIOS VS. MARK–RECAPTURE: A COMPARISON OF ASSUMPTIONS

As many ecologists are quick to point out, the use of mark–recapture estimators also requires a number of assumptions to hold for resulting estimates to be valid. For instance, researchers often must assume that mortality and emigration/immigration do not occur during sampling, that marks are not lost or recorded incorrectly, that survival and sampling processes are similar for like individuals, and that the fates of individuals are independent (see Williams et al. [2002] for a complete description of assumptions required for specific models).

When using mark–recapture, one can often minimize assumption violations by using an appropriate sampling design. In contrast to abundance estimation, undetected heterogeneity in detection probabilities among individuals produces only small bias in survival estimators (Williams et al. 2002). Sources of variation in detection probability and survival also can be incorporated into competing models and identified for a particular data set using model selection metrics such as AIC (Burnham and Anderson 2002). Uncertainty in the model selection process can be accounted for by averaging estimates over models (Buckland et al. 1997). Finally, the data collected for mark–recapture can be used to perform goodness-of-fit tests to assess whether or not there are any outstanding assumption violations that have not been addressed.

None of these precautions for dealing with assumption violations has been implemented, to our knowledge, for age ratios computed from museum collections (but see Udevitz and Ballachey 1998). The investigator not only must claim similar ecology, dynamics, and population trajectories of populations being compared, but also must claim knowledge about the dynamics of museum collectors. That is, museum collectors must sample the populations in question similarly with respect to age, even though personal preferences of the collector and the accessibility of different habitat types may differ from site to site, and quite possibly, with latitude and other covariates of interest.

DISCUSSION

As articulated by Clobert and Lebreton (1991), age-based methods alone are simply insufficient for estimating survival for bird populations because they do not incorporate enough realistic elements of the sampling process. We have shown that life table methods such as those proposed by Ricklefs (1997), if used in survival estimation, are prone to producing a ''highly precise, incorrect answer'' (Anderson et al. 1981). We have two recommendations for avian ecologists interested in survival estimation. First, if logistical considerations really dictate use of age ratio approaches, then we recommend use of the formal modeling framework provided by Udevitz and Ballachey (1998), rather than ad hoc approaches. Second, we recommend serious consideration of the various formal approaches to capture–recapture modeling that deal with animal movement. Although methods based on mark–recapture do not provide easy answers to every problem, we believe that these methods are far superior to ad hoc age ratio methods. The variety of mark–recapture alternatives explored here permits avian ecologists flexibility to address many questions of interest about avian demography. We anticipate that further methodological developments, together with advances in monitoring technology by innovative ornithologists, will increase the flexibility and affordability of robust sampling methods for avian species. We can all agree that questions concerning survival are some of the most interesting and important in avian ecology and evolution. However, they are often fundamentally difficult to address . . . and there is no such thing as a free lunch.

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APPENDIX A

The derivation of age ratio estimator bias under aging error is available in ESA's Electronic Data Archive: *Ecological Archives* E086-134-A1.

APPENDIX B

A description of mark–recapture models useful for avian survival estimation citing case studies is available in ESA's Electronic Data Archive: *Ecological Archives* E086-134-A2.

COMPARATIVE DEMOGRAPHY OF NEW WORLD POPULATIONS OF THRUSHES (TURDUS SSP.): REPLY

Robert E. Ricklefs[1,3] and Sievert Rohwer[2]

Conn, Doherty, and Nichols (2005), hereafter CD&N, question the wisdom of using age ratios obtained from museum collections to estimate adult survival rates in populations of birds. Ricklefs (1997), Rohwer (2004), and other studies that have used this approach have been careful to recognize and evaluate potential problems, to the extent possible. The basic assumptions of the method are that adult and first-year birds can be distinguished reliably and that their survival rates do not differ at the time during the annual cycle when the age ratio is estimated. Additional issues discussed by Ricklefs (1997) were potential biases arising from nonstable (growing or declining) populations, varying population size, collecting biases favoring adults or immatures, aseasonal breeding, senescent de-

[1] Department of Biology, University of Missouri–St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121-4499 USA.

[2] Burke Museum, Box 353010, University of Washington, Seattle, Washington 98195-3010 USA.

[3] E-mail: ricklefs@umsl.edu

cline in survival rate, and delayed plumage maturation. To some extent, these biases can be evaluated from museum data, for example by seasonal differences in the ratios of adult to first year birds; species with marked delays in plumage and behavioral maturation that would influence collecting can be avoided. Ricklefs (1997) considered that these potential biases individually were unlikely to be strong, but it was not possible to estimate most of them directly. Nonetheless, age ratios have been useful in comparative studies for estimating average adult survival in populations sampled broadly in time and space. For this purpose, collection-based methods will often outperform local banding studies, which are sensitive to individual dispersal movements. The latter are better suited to addressing more detailed, localized issues such as variation in survival over time or with age.

Perhaps the most fundamental difference between our approach and that of CD&N is our faith in the quality of the data. To be sure, the recapture of a banded bird conveys a certainty about the survival of an individual over a specified period that can be used to build a model of the survival of individuals in a population. The presence of a specimen in a museum collection is a unique observation lacking any direct reference to an earlier point in its life. Although such samples are not suited to longitudinal analyses based on models incorporating probabilities of survival and resighting of individual birds, our statistical methods do provide an estimate of survival for populations where banding approaches are not possible. Many studies in comparative demography will be practical and economical only with the unique resources of museum collections. The data from these collections are better than CD&N claim. Geographically wide-ranging sam-

ples collected over decades, as in Ricklefs' analysis of thrushes and Rohwer's study of warblers, circumvent problems of local dispersal and short-term variation in demography that might otherwise introduce biases. Ornithologists should recognize that band-return approaches also require considerable (often unjustified) faith in unbiased net capture, in emigration being a negligible factor, and in the global applicability of locally estimated parameters. Moreover, the power of mark–recapture methods often greatly exceeds the quality of the data used to feed them.

Additional concerns about the use of age ratios expressed by CD&N derive from biases related to aging error, immigration and emigration, and the uncertainty associated with assumptions about these variables. We comment on these issues in turn. Estimating survival from age ratios requires an accurate age criterion. Because plumage characters most commonly provide these criteria, this depends on careful evaluation of molt cycles. In many cases, suitable plumage markers of age class are not available and age ratios cannot be used. Certainly many of the aging criteria described in banding manuals, such as Jenni and Winkler (1994) and Pyle (1997*a, b*), are only approximate and do not reliably allow all individuals to be assigned to age class (see, for example, Green [2004]). For many parts of the world, details of feather markings that change with plumage cycles and the limits of incomplete molts, and that allow individuals to be assigned to age classes, are poorly known. However, for Townsend's and Hermit Warblers (*Dendroica townsendi* and *D. occidentalis*), plumage characters reliably distinguish first-year and adult males (Jackson et al. 1992, Rohwer 2004). One of the reasons for working with New World species of the genus *Turdus* was a reliable plumage marker that separates immature birds through most of their first year from birds that are at least one year old (Ricklefs 1997). The marker works less well with some Old World species of *Turdus* that retain elements of immature-like plumages as adults (e.g., Song Thrush *Turdus philomelos*; Jenni and Winkler 1994). As CD&N rightly imply, the age ratio technique for museum specimens is not for every species, and probably not for most; further, it may not work for both sexes of a species, because age-related characters are frequently more difficult to assess in females than in males.

The purported bias from immigration and emigration puzzles us. When museum collections sample populations broadly across the range of a species, movement of individuals from one place to another is not an issue. Even for local populations, CD&N's analysis of immigration and emigration seems misleading. It should be evident that if adults and immatures were to move with equal probability, their proportion would not be altered by immigration or emigration, provided that their relative numbers were homogeneous across the metapopulation. CD&N argue otherwise. They define the proportion of individuals with adult plumage in a population after one year of survival and emigration/immigration as $v_{i+1} = \phi_i[F_i + \pi_i(1 - F_i)]$. In this relationship, ϕ_i is the annual survival rate at time i; F_i is a fidelity parameter, i.e., the proportion of individuals that stay at home; and π_i is the rate of immigration relative to that of emigration. Accordingly, the proportion of adult-plumage individuals equals the annual adult survival rate only when there is no movement ($F_i = 1$) or when immigration equals emigration ($\pi_i = 1$). However, CD&N derived this equation supposing that population size is constant, i.e., growth rate $\lambda = 1$, and they therefore calculated the age ratio $v_{i+1} = N^A_{i+1}/(N^A_i + N^I_i)$, where N^A and N^I are the numbers of adult and immature individuals. This is the ratio of adults in one year to the sum of adults and immature individuals in the previous year. In practice, the age ratio is calculated from specimens obtained at the same time and $v_{i+1} = N^A_{i+1}/(N^A_{i+1} + N^I_{i+1})$. Thus, CD&N confound population change with immigration and emigration. For populations in which births and deaths balance, there is no bias when $\pi_i = 1$; when $\pi_i \neq 1$, population size is not constant.

Of course, adults and immatures in some populations move with different probabilities from one region, or habitat, to another. Thus, Graves (1997) and Rohwer (2004) were careful to argue that changes in age ratios along habitat or density gradients across small distances were likely to represent despotic breeding distributions (Fretwell 1972), rather than differences in survival. In this case, only banding studies can assess differential movement by adults and immatures, but one would have to distinguish immature (1-year-old) and adult ($\geq$2-year-old) individuals because despotic habitat distribution models assume that first-year birds will be prevented from settling in high-quality habitat. Thus, adults replace adults in such habitats, resulting in a net immigration of adults (Rohwer 2004). Plot-based banding studies on mechanisms of habitat distribution therefore would require an assessment of age, which can be determined only by plumage markers where young disperse from their natal area. Moreover, for species that are rarely recovered or resighted outside of study plots, such studies would be easier to justify if the appropriate geographic scale and habitat gradient were first obtained from museum data. CD&N cite the study of Cilimburg et al. (2002) on Yellow Warblers (*Dendroica petechia*), in which the investigators searched over widely distributed banding plots to increase the probability of resighting dispersed individuals, thus raising the survival estimate. Nonetheless, their estimate was not high enough for the Bitterroot Valley population to be stable, even though the

investigators could have detected location shifts up to 45 km (but could not possibly have searched the entire area) (Cilimburg et al. 2002). An estimate of annual survival based on a regional sample of age ratios would have provided a proper context for evaluating emigration and the source vs. sink status of the Bitterroot population.

CD&N's uncertainty analysis emphasizes sources of variation in estimates of annual survival from age ratios, which is appropriate, but it overstates the problem. Variation in fidelity (F_i) and the immigration/emigration ratio (π_i) do not contribute to variation in the estimate of local adult survival, except through their effect on population growth rate, and not at all on global estimates of survival. CD&N's pencil-and-paper example incorporated a range in variation in λ of up to $\pm$ 0.24, certainly beyond typical values in natural populations. Ricklefs (1997) also discussed biases in estimated adult survival resulting from variation in population growth and collecting bias, although his estimates of standard errors did not incorporate these effects. CD&N cite the example of the growth rate of a local Canadian population of the Cerulean Warbler (*Dendroica cerulea*), claimed to be rapidly declining (λ = 0.73) by Jones et al. (2004). This study highlights the challenge of estimating adult survival from band-return analyses. The estimated adult survival (ϕ = 0.49 $\pm$ 0.05) was based on 74 resightings of banded males over a six-year study concentrated on 30 ha of forest, with annual variation in estimated ϕ_i ranging between ~0.35 and 0.80. In another cited study, in this case of the Ciril Finch (*Serinus citrinella*), based on 1383 recaptures over nine years in two study populations, Senar et al. (2002: Table 2) found that the 95% confidence limits for adult survival in one set of models extended beyond 0 and 1. Thus, uncertainty is a problem with the estimation of survival, regardless of the approach. We agree with CD&N that sources of uncertainty beyond binomial sampling should be addressed to the extent possible in any study of population processes.

In spite of advances in mark–recapture methodology, including the incorporation of permanent emigration into these models, the realities of survival estimation are that recapture approaches are nonetheless plagued by lack of access to most populations for banding studies, uncertainties about emigration in most cases, and localization in both time and space. Museum methods based on age ratios in collections avoid these problems because sampling can be extensive across space and time, but they incur uncertainties with respect to age estimation, sampling bias, and population growth rate. In addition, they rarely allow hypothesis testing with respect to year, condition, and age-related survival, although such effects could be analyzed with suitable samples (cf., for example, Loison et al. 2002). Age ratio analysis is amenable to likelihood approaches (e.g., Udevitz and Ballachey 1998). Indeed, the age ratio is an unbiased maximum likelihood estimator of adult survival rate, and its analysis can be adapted to test additional effects in a likelihood framework.

As CD&N point out, age ratios must be used with care to estimate survival rates. The same is true of mark–recapture data. The sophistication of mark–recapture models cannot reduce potential biases, uncertainties, and sampling limitations inherent in the data themselves. Nor could mark–recapture models be applied, for example, to a hemispheric analysis of survival in 30 populations of 19 species ranging from Alaska to Patagonia, as in the case of Ricklefs's (1997) study of *Turdus*, or to the kinds of questions regarding populations of hybridizing warblers throughout their ranges and over elevation gradients posed by Rohwer (2004). While CD&N argue that they could construct scenarios that would invalidate these comparisons, they could neither test these ad hoc scenarios statistically nor deny the close match between survival estimates from age ratios and band-return data for well-studied north temperate populations of *Turdus* and *Dendroica*. Any estimate of survival probability has associated uncertainty. Different approaches are suitable for different questions. We hope that students of population statistics will recognize the potential of using age ratios to estimate survival where this cannot be addressed by banding studies, and that they will work to evaluate potential sources of uncertainty and refine underlying models.

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